IV.—*On the Structure of the Larvæ and the Systematic Position of the Genera* Mycetobia, *Mg.*, Ditomyia, *Winn.*, *and* Symmerus, *Walk.* (*Diptera Nematocera*). By D. Keilin, D.Sc. (from the Quick Laboratory, University of Cambridge).

[Plates II.–V.]

I. *Mycetobia pallipes*, Meigen.

The larvæ of *Mycetobia pallipes* were first described and figured by Lyonnet (1832) and Guérin-Méneville (1835).

Dufour (1844) and notably Perris (1870), after a more complete study of these larvæ, showed that their respiratory system is amphipneustic and called attention to their external resemblance to the larvæ of *Rhyphus fenestralis*, Scop.

Osten-Sacken (1892), referring to the papers of these entomologists, again raised the question of the larval resemblance of *Mycetobia* and *Rhyphus*, which in the adult stage seemed to be so different. But since Osten-Sacken the majority of entomologists dealing with *Mycetobia* unquestioningly referred this genus to the family Mycetophilidæ, passing over in silence the peculiar structure of its larvæ. Those who gave the matter any attention either doubted the correctness of the original observations of Dufour and Perris, or did not admit the value of larval characters in determining the systematic position of Insects.

However, a study of the life-history and larval morphology of *Mycetobia pallipes*, Mg., and *Rhyphus fenestralis*, which I carried out in 1912–13 on material collected at Chaville (near Paris) has led me to the conclusion that the resemblance between these larvæ and their difference from those of Mycetophilidæ is much deeper than was ever supposed.

In the present paper I will point out only the main characters common to the early stages of *Mycetobia pallipes* and *Rhyphus fenestralis*, but not found in those of Mycetophilidæ.

A more detailed study of the larval anatomy of *Mycetobia* I propose to reserve for a special paper dealing with the family Rhyphidæ.

Characters common to *Mycetobia pallipes* (Pl. II. fig. 2, Pl. V. figs. 36, 37, 38) and *Rhyphus fenestralis* (Pl. II. fig. 1).

1. The eggs are invested with a gelatinous mass which is fixed to a solid substratum.
2. Eggs are pear-shaped.

Characters common to all the Mycetophilidæ (Pl. III.) except the genera *Ditomyia* and *Symmerus*.

1. Eggs are more or less scattered on the surface of the fungus or rotten wood.
2. Eggs are elongated or subspherical.

3. Embryo in the egg curved.
4. The larvæ move in a serpentine manner, or by means of very active mandibles.
5. The segments of the body are separated by intercalary rings (Pl. V. fig. 38).

6. The larval head with a pair of tentorial rods (Pl. II. figs. 1 & 2, *t.n.*) similar to those of the larvæ of *Trichocera*.
7. Antennæ with a special sensory organ (Pl. V. fig. 37, *b.s.*), corresponding to the bell-shaped papilla of many other dipterous larvæ (for instance, those of *Ditomyia* and all cyclorhaphous Diptera) and with some small cylindrical papillæ.
8. Mandibles (Pl. V. figs. 35 & 36) show two distinct portions: basal portion (*b.p.*) with an internal hook (*h.*), and terminal or apical portion (*t.p.*) which is more chitinised, ending in three teeth and bearing two brushes of brown setæ.
9. Maxillæ fleshy and soft; the maxillary palp (figs. 1 & 2, *m.p.*) broad, thick, transparent, bearing two groups of sensory papillæ (*a.* and *b.*); the internal part of the maxillæ (*m.x.*), besides a few sensory organs, bears numerous long setæ.
10. Labrum with two mid-ventral protuberances covered with hairs (figs. 1 & 2, *l.r.* & *p.r.*) and a small comb-shaped plate (*c.m.*) on each side of posterior protuberance.
11. Labium well developed and with distinct labial palps (*l.p.*).
12. The thoracic sensory organs which are the remains of the thoracic legs are composed of four hairs (two long and two short).

3. Embryo straight.
4. The larval movements are worm-like.

5. No distinct intercalary rings (Pl. III. fig. 3); only some larvæ—for instance, those of *Ceroplatus*—have the segmentation of their abdomen masked by superadded transversal folds.
6. Head without tentorial rods.

7. Antennæ either elongated as in *Bolitophila* (Pl. III. fig. 4, *A.n.*, and fig. 13) or reduced to a flat, wide, non-chitinised surface bearing some very small sensory papillæ.

8. Mandibles (figs. 5 & 7) flattened, strongly chitinised, and with their internal margin toothed.

9. Maxillæ (Pl. III. figs. 10, 11, 12) flattened and strongly chitinised, with their internal margin (*m.x.*) toothed, like those of the mandibles. The maxillary palps (*m.p.*) are very much reduced.

10. Labrum (figs. 6 & 8) without mid-ventral protuberances and without comb-shaped plates.

11. Labium reduced and not visible from exterior.

12. Thoracic sensory organs composed of four hairs of equal length (fig. 9).

13. Respiratory system is amphipneustic with only two pairs of functional spiracles: (1) prothoracic and (2) postabdominal.	13. Respiratory system is either hemipneustic (fig. 3) with one pair of prothoracic and seven pairs of abdominal spiracles, or propneustic (*Polylepta* or *Diadocidia*), or apneustic (*Ceroplatus*).
14. Alimentary duct without anterior cœca.	14. Alimentary duct with a pair of anterior lateral cœca.
15. Anus ventral.	15. Anus terminal or subterminal.
16. Salivary glands short.	16. Salivary glands very long.
17. Hypoderm of posterior segments of larvæ, which surrounds the anal cleft, is composed of very large and thick cells.	17. No special large cells in hypoderm of the posterior end of the body.
18. Pupæ strongly chitinised with rows of small hooks on the abdominal segments and especially on the posterior end of their body.	18. Pupæ with thin chitin and without the *rows* of short spines or hooks.

All these characters show us clearly that the difference between the larva of *Mycetobia* and those of Mycetophilidæ (s. l.) is as striking as its resemblance to the larvæ of Rhyphidæ.

But to solve finally this question a comparative study of the adult stages of these Diptera had to be undertaken, and this was done by F. W. Edwards (1916, p. 115), who in his interesting paper "On the Systematic Position of the Genus *Mycetobia*, Mg.," arrived at the following conclusion :—

"*Mycetobia* agrees with the Rhyphidæ and diverges from the Mycetophilidæ in the possession of a large gular plate, in the structure of the second palpal joint, in the position of the forking of the radial vein, the course of the cubital vein, and in the chitinous spermathecæ of the female. Since the venation of *Mycetobia* has been shown to be directly derivable from that of the Rhyphid genus *Olbiogaster*, it is probable that any resemblances in this respect to the Mycetophilidæ are due to convergent evolution, and not to relationship. The genus *Mycetobia* (and with it *Mesochria*, though not *Ditomyia* or *Symmerus*) must therefore, on grounds of adult as well as larval structure, be transferred from the Mycetophilidæ to the Rhyphidæ."

II. *Ditomyia fasciata*, Meig.

The first indication of the habitat of this species we owe

to Meigen (1818, t. i. p. 230), who found a young undeveloped male of this fly in *Polyporus versicolor*.

Zetterstedt (1851, t. x. p. 4071) quotes Behrens, who bred this insect from a fungus which he found on *Juglans regia*.

According to Winnertz (1863, p. 669), the larvæ of *D. fasciata* live in different *Polyporus* and especially in *P. versicolor* and *ferrugineus*; he quotes also Kaltenbach who bred *D. macroptera*, Winnertz, from *Polyporus ignarius*.

Schiner (1864, i. p. 428) reared *D. fasciata* from various Polypori.

Frauenfeld (1866, p. 200) found the larvæ of this species in *Polyporus squamosus*; he also gave the first description of the larval and pupal stages of this fly. Unfortunately, his very short description does not contain any figure, and may be applied to many other dipterous larvæ. The only characters of his description worth mentioning are the following: (1) the intersegmental spaces are deeply constricted, (2) the first segment of the thorax is large, and (3) the posterior end of the body bears two protuberances ended by a sharp spine.

We have, finally, to mention that the collection in the Entomological Museum of Cambridge contains the pupæ and adults of *Ditomyia fasciata*, Mg., reared by Fryer (1910) from *Polystictus versicolor* collected at Chatteris (Cambs) and by H. Scott (1910) from the same fungus collected from beech-stumps at Henley-on-Thames.

I received the larvæ and pupæ of *Ditomyia fasciata*, which will be described here, from Mr. F. W. Edwards, who found them in a fungus, which he believes to be *Polystictus versicolor*, growing on old beech-stumps near Cambridge and at Baldock, Herts.

Later on, I collected myself a few of these larvæ in a piece of wood covered and penetrated by the mycelium of a fungus.

According to Edwards, in nature the larvæ usually live upon the old fungi, but in his breeding-jars he observed them attacking the fresh fungi also.

The larvæ are opaque white in colour and have very little power of movement. Pupation takes place within the fungus without the formation of any cocoon; before the emergence of the adult the pupa bores its way to the surface and comes halfway out.

The larva is 9·3 mm. long, with very deep intersegmental grooves (Pl. IV. fig. 14).

The head of the larva is completely free, though it may be retracted in the first thoracic segment. The antennæ (Pl. IV. fig. 23) are very small and consist of a short basilar segment which bears sensory organs of three different shapes: (1) the main bell-shaped (*b.s.*) sensory organ which is very common in dipterous larvæ, (2) one bi-articulated papilla (*p.*), and (3) five short cylindrical papillæ.

The labrum (fig. 15) shows on its anterior margin a brush composed of ordinary setæ mixed with sensory hairs. On each of its latero-anterior corners it bears a bidental chitinous plate (*d.*), and on its ventral side a series of short spines and scales and two strongly chitinised plates (*p.l.*).

The mandibles (fig. 22) are very well developed, thick, and of a dark brown chitin; their external margin is slightly cut into four teeth; they bear three lateral sensory hairs and a brush of ordinary brown setæ which originates from the internal basilar corner of the mandibles.

The maxillæ (fig. 17). The basal part or cardo of the maxillæ consists of soft and transparent chitin with a transverse brown band (*t.b.*) and a sensory organ in the form of a small circular groove. The internal part of the maxillæ (*m.x.*) is conical in shape and bears a long sensory hair (*s.h.*). The maxillary palp (*m p.*) is very well developed and furnished with a series of sensory organs and some ordinary chitinous setæ.

The labium consists of a short chitinous plate terminating in two tridental processes. On the ventral side it bears two hemispherical palps (*l.p.*) of transparent chitin, each with three sensory papillæ.

The thorax is composed of three large segments furnished with a series of sensory hairs. Among the latter we may mention six groups of three hairs (fig. 19) which represent the remains of the thoracic legs. As I have previously shown (1911, 1915) these six groups of sensory organs exist in all dipterous larvæ and are always in direct connection with imaginal discs of the thoracic legs.

The eight abdominal segments bear also a series of sensory hairs, and on their ventral side they are furnished with lozenge-shaped projections or pseudopodia covered with very short setæ. The last abdominal segment differs from all the others in bearing the anus and a pair of dorsal projections terminated by spiracles.

The respiratory system of this larvæ is peripneustic, *i. e.* it is composed of nine pairs of functional spiracles (one pro-

thoracic and eight abdominal), and one pair of metathoracic non-functional spiracles connected with the main tracheal trunks by means of simple chitinous bands.

All the functional spiracles, except the last abdominal, are circular, with numerous trema surrounding a central chitinous plate which corresponds to the cork-shaped scar ("Bouchon cicatriciel") of the spiracles of *Trichocera*, Tipulid or Bibionid larvæ. The prothoracic spiracle (fig. 21) is much larger in size than any of the first seven pairs of abdominal spiracles (fig. 18).

The posterior abdominal spiracles (fig. 20, *s.p.*), which are situated on the dorsal projections of the last abdominal segment, are elongated and spine-shaped. The surface of their external scar (*s.c.*) is covered with very small chitinous hooks.

Alimentary canal (fig. 16). The very short pharynx is enclosed in the larval head. It is followed by a short œsophagus (*o.e.*) which enters the proventriculus (*pr.*). Two long lateral cœca (*a.c.*) arise from the anterior part of the midgut, just behind the proventriculus and, directed backwards, are tightly applied to the lateral sides of it. The midgut (*m.g.*) is in the form of a straight cylindrical tube. The four Malpighian tubes (*M.*) arise separately at the junction of the mid- and hind-gut. These four tubes lie in the posterior part of the body and surround the hind-gut.

The salivary glands (*s.g.*) are tubular and extend a small distance behind the posterior end of the anterior cœca.

The pupa (Pl. IV. fig. 24) is 8 mm. in length, completely free from the larval skin, and brown in colour. The head is much recurved on the ventral side, and the thorax, which projects forward, bears a pair of prothoracic respiratory horns (*p.h.*). The legs of the pupa are not superposed as is often the case in dipterous pupæ, but lie in the same plane. Each abdominal segment bears dorsally a row of short spines. The last segment (Pl. IV. fig. 25) is furnished with five pairs of hooks curved dorsally.

III. *Symmerus annulata*, Meigen.

All our knowledge of the larvæ of *Symmerus* was contained in a short sentence of Winnertz (1863, p. 671), who bred "one female from a larva which lived in a decomposed fungus on *Carpinus betulus*."

During the month of May of this year Mr. Edwards in-

formed me that he had found a specimen of *Symmerus annulata* which had hatched in one of his breeding-jars. "The larvæ of this species," he added in his letter, "were boring in a piece of rotten elm wood. They are almost transparent and glassy in appearance, and, like those of *Ditomyia*, move very little and very slowly. The pupæ wriggle in an almost snake-like manner when extracted from their habitat. Unfortunately I found that all the full-sized larvæ had pupated. I have one larva preserved in spirit."

All the material Mr. Edwards could send me consisted of an empty pupa with a moulted larval skin attached to it and the larva preserved in spirit, mentioned in his letter.

This was, however, quite sufficient for the complete morphological study of this larva.

The larva of *Symmerus annulata* (Pl. V. fig. 26) is 11 mm. in length; its last abdominal segment bears the posterior spiracles, but is without the dorsal paired prominences which are present in *Ditomyia* larvæ. These two larvæ are easily distinguished from one another by their colour and post-abdominal prominences, but they are quite similar in the detailed structure of almost all their organs.

The antennæ (Pl. V. fig. 32), labrum (fig. 27), mandibles (fig. 31), maxillæ (fig. 29, *m.x.*), and labium (fig. 29, *l.b.*), with their palps (*m.p.*, *l.p.*) have the same structure as those of *Ditomyia* larvæ. The differences in detail of these organs in these two larvæ are shown in the above-mentioned figures.

We may mention only that in the maxillary palps of *Symmerus* larvæ we do not find the lateral sensory papilla which is well developed in *Ditomyia* larvæ (Pl. IV. fig. 17, *l.s.*). The labium in *Symmerus* larvæ is more rounded.

The thoracic and abdominal segments also bear the sensory hairs, and the remains of the thoracic legs are represented by three sensory hairs (fig. 30).

The last abdominal segment is rounded.

The respiratory system is peripneustic, with nine pairs of functional spiracles: one prothoracic and eight abdominal.

The spiracles (figs. 33 & 34) are very small, and their structure is similar to those of the first seven pairs of abdominal spiracles of *Ditomyia*.

Pupæ (fig. 28). Unfortunately I have only one empty skin of a pupa. I may mention, however, that the prothoracic horns are more elongated than in the pupa of *Ditomyia*, and that the thoracic segments bear a row of lateral short hooks.

The study of the larvæ and pupæ of *Ditomyia* and *Symmerus* shows clearly the great similarity in structure of nearly all their organs. It also shows, on the other hand, that the larval and pupal structure of these two genera is totally different from that of all the Mycetophilidæ.

The difference is especially striking in the structure of the antennæ, mandibles, maxillæ, and labium, with their palps, the sensory organs, respiratory system, structure of the spiracles, the salivary glands, and, finally, the form of the pupæ.

These two genera must therefore be re-united in a special family, the Ditomyidæ, which itself must be completely separated from the family of the Mycetophilidæ.

From the study of the larval and pupal characters it follows that the family Ditomyidæ must occupy among the Diptera Orthorrhapha Eucephala, of Brauer, a position equally important with that of the Mycetophilidæ, Bibionidæ, Rhyphidæ, &c.

As to the relations of this new family to the others we can state only that the larvæ of Ditomyidæ bear a closer resemblance to the larvæ of Bibionidæ than to those of any other Diptera, and more especially when we compare their labra, mandibles, maxillæ, and the structure of the spiracles.

The subfamily Mycetobiinæ of Winnertz (1861), composed of the genera *Mycetobia*, *Mesochria*, *Ditomyia*, and *Symmerus*, must therefore completely disappear, as *Mycetobia* (and with it, according to Edwards, *Mesochria*) must be transferred to the Rhyphidæ; while the two others go to form a separate family, Ditomyidæ, completely separated from Mycetophilidæ.

I must express here my best thanks to Mr. F. W. Edwards for sending me the specimens of *Ditomyia* and *Symmerus* larvæ. I may say that it is his re-discovery of these larvæ which has enabled me to accomplish this study.

References.

Dufour L. (1849.) "Histoire des Métamorphoses du *Rhyphus fenestralis* et du *Mycetobia pallipes*." Ann. de la Soc. Entom. de France, 2e série, t. viii. pp. 195–210, pl. 7.

Edwards, F. W. (1916.) "On the Systematic Position of the Genus *Mycetobia*, Mg. (Diptera Nematocera)." Ann. & Mag. Nat. Hist. ser. 8, vol. xvii. pp. 109–116.

——. MS. Notes on *Ditomyia* and *Symmerus*, see pp. 36 & 39 of this paper.

Frauenfeld, G. R. von. (1866.) Zoologische Miscellen. VII. "Beschreibung der Larven und Puppen von *Ditomyia fasciata*, Mg." Verh. der k. k. zool.-bot. Gesellsch. Wien, Bd. xv. p. 200.

Guérin-Méneville, F. E. (1835.) Iconographie du Règne Animal de G. Cuvier, t. ii. Planche 93, figs. 3–5.

Keilin, D. (1911.) "Sur certains organes sensoriels des larves des Diptères et leur signification probable." C. R. Acad. Sciences, Paris, t. 153, p. 977.

——. (1912.) "Recherches sur les Diptères du genre *Trichocera*. Biologie, Développement, Affinités." Bullet. Scient. de la France et Belgique, 7e série, t. xlvi. Fasc. 2, pp. 172–192, pls. v.–viii.

——. (1915.) "Recherches sur les larves de Diptères Cyclorhaphes." Bullet. Scient. de la France et Belgique, 7e série, t. xlix. Fasc. 1–2, pp. 15–198, pls. i.–xvi.

Lyonet, P. de. (1832.) "Recherches sur l'Anatomie et les Métamorphoses de différentes espèces d'Insectes." Ouvrage posthum. publié par M. W. de Haan. Paris, J. Ballière, 580 pp., 54 Planches. (See pp. 186–189, 562, and pl. 17.)

Meigen. (1818.) Systematische Beschreibung der bekannten Europäischen zweiflügeligen Insekten.

Osten-Sacken, C. R. (1892.) "On the Characters of the Three Divisions of Diptera Nemocera: *Nemocera vera*, *Nemocera anomala*, and *Eremochæta*." Berl. entom. Zeitschr. Bd. xxxvii. pp. 417–466.

Perris, E. (1870). "Histoire des Insectes du Pin maritime." Ann. de la Soc. Entom. de Fr. 4me série, t. x. (See pp. 186–196, pl. 2. figs. 47–61.)

Schiner. (1864.) Fauna Austriaca, t. i. p. 428.

Winnertz, J. (1863.) Beitrag zu einer Monographie der Pilzmücken." Verh. Zool.-Bot. Gesellsch. Bd. xiii. pp. 637–964. (See pp. 669–671.)

Zetterstedt. (1851.) Diptera Scandinaviæ.

EXPLANATION OF THE PLATES.

Plate II.

Fig. 1. Head of the larva of *Rhyphus fenestralis*, Scop., ventral aspect. *a.* and *b.*, sensory organs of maxillary palp; *c.m.*, comb-shaped plate of labrum; *l.p.*, labial palp; *l.r.*, labrum with its anterior ventral prominence; *m.d.*, mandibles; *m.p.*, maxillary palp; *m.x.*, maxilla; *p.r.*, posterior ventral prominence of labrum; *t.n.*, tentorial rods.

Fig. 2. Head of the larva of *Mycetobia pallipes*, Mg. Letters as in fig. 1.

Plate III.

Fig. 3. Larva of *Mycetophila blanda*, Winn., viewed laterally.

Fig. 4. Head of the larva of *Bolitophila fusca*, Meig.; dorsal aspect. *A.n.*, antennæ; *E.*, eyes.

Fig. 5. Mandible of *Mycetophila blanda*, Winn.

Fig. 6. Labrum of *Bolitophila fusca*, Meig.

Fig. 7. Mandible of *Mycomyia marginata*, Meig.

Fig. 8. Labrum of *Mycomyia marginata*, Meig.
Fig. 9. Pleural sensory organ representing the remains of thoracic legs of *Mycomyia marginata*, Meig.
Fig. 10. Maxilla of *Mycomyia marginata*. *m.x.*; *m.p.*, maxillary palps.
Fig. 11. Maxilla of *Bolitophila fusca*, Meig.
Fig. 12. Maxilla of *Mycetophila blanda*, Winn.
Fig. 13. Antenna of *Bolitophila fusca*, Meig.

Plate IV.

[All the figures of this Plate concern the larva and pupa of *Ditomyia fasciata*.]

Fig. 14. Larva of *Ditomyia fasciata*, viewed laterally.
Fig. 15. Labrum, ventral side. *d.*, dental chitinous plate; *p.l.*, ventral plate.
Fig. 16. Alimentary canal of the larva. *a.c.*, anterior cœca; *m.g.*, mid-gut; *M.*, Malpighian tubes; *o.e.*, œsophagus; *p.r.*, proventriculus; *s.g.*, salivary glands.
Fig. 17. Maxillæ and labium of larva. *l.b.*, labium; *l.p.*, labial palps; *l.s.*, lateral sensory organ of the maxillary palp; *m.p.*, maxillary palp; *m.x.*, maxillæ; *t.b.*, transversal chitinous band of the cardo of maxilla; *s.h.*, sensory hair of the internal lobe of maxillæ.
Fig. 18. Abdominal spiracle of larva.
Fig. 19. Sensory organ—remains of thoracic leg.
Fig. 20. Last pair of abdominal spiracles. *f.c.*, felt-chamber ("chambre feutrée"); *T.r.*, tracheal trunks; *s.c.*, external scar; *s.p.*, spiracles.
Fig. 21. Prothoracic spiracle—the black surface represents the external scar of this spiracle.
Fig. 22. Mandibula.
Fig. 23. Antenna. *b.s.*, bell-shaped sensory organ; *p.*, biarticulated papilla.
Fig. 24. Pupa, viewed laterally. *p.h.*, prothoracic respiratory horns.
Fig. 25. Posterior end of this pupa, showing the hooks.

Plate V.

[Figs. 26–34 concern larva and pupa of *Symmerus annulata*.]

Fig. 26. Larva of *Symmerus annulata*, viewed laterally.
Fig. 27. Labrum of the larva. Letters as in fig. 15.
Fig. 28. Pupa of *Symmerus annulata*.
Fig. 29. Maxilla and labium of this larva. Letters as in fig. 17.
Fig. 30. Sensory organ—remains of thoracic leg.
Fig. 31. Mandible.
Fig. 32. Antennæ. Letters as in fig. 23.
Fig. 33. Abdominal spiracle.
Fig. 34. Last abdominal spiracle.
Fig. 35. Mandible of the larva of *Rhyphus fenestralis*.
Fig. 36. Mandible of the larva of *Mycetobia pallipes*.
Fig. 37. Antenna of *Mycetobia pallipes*.
Fig. 38. Larva of *Mycetobia pallipes*, viewed dorsally.